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PHYLOGENY OF *CERATOSOMA* (NUDIBRANCHIA: CHROMORIDIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: Two new species of *Ceratosoma* are described. *Ceratosoma ingozi* is known only from deep water off the temperate coast of South Africa. *Ceratosoma alleni* is known from shallow reefs in the Philippine Islands. The phylogenetic relationships of the species of *Ceratosoma* are discussed. *Ceratosoma ingozi* is relatively plesiomorphic in most aspects of its morphology and appears to be most closely related to two other species known from southern Australia. *Ceratosoma alleni* is highly derived in several aspects of its morphology and appears most closely related to *C. moloch*, also from the Indo-Pacific tropics.

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INTRODUCTION

The anatomy and systematics of members of the genus *Ceratosoma* Gray have been recently reviewed (Rudman, 1988). Seven distinct species have been recognized and the systematic status of one other remains unresolved. Baba (1989) considered *C. bicolor* as an eighth distinct species, although he stated that there was a need for further study of additional specimens.

An undescribed species of *Ceratosoma* was recorded from South Africa by Gosliner (1987). Since then, an additional undescribed species has been discovered from the Philippine Islands. This paper describes these new species, their morphology and phylogenetic position.

Specimens deposited in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco are designated by the abbreviation CASIZ. Specimens deposited in the Department of Marine Biology of the South African Museum, Cape Town are designated by the abbreviation SAM.

SPECIES DESCRIPTIONS

Ceratosoma ingozi sp. nov. (Figs. 1A, 2, 3)

Ceratosoma sp. Gosliner, 1987:85, fig. 138.

TYPE MATERIAL. — Holotype: SAM A36012, off Danger Point, Walker Bay, Cape Province, South Africa, 44 m depth, 16 April 1984, W. R. Liltved. Paratype, CASIZ 104199, one specimen, same locality and date as holotype. Paratypes, SAM A36011, four specimens, one dissected, off Danger Point, Walker Bay, Cape Province, South Africa, 26 m depth, 24 April, 1984, W.R. Liltved. Paratypes, SAM A36009, one specimen, off Danger Point, Walker

Bay, Cape Province, South Africa, 34 m depth, 11 April 1984, W. R. Liltved.

ETYMOLOGY. — *Ceratosoma ingozi* is derived from the Xhosa word for danger, *ingozi*, since this species has only been found from Danger Point.

DISTRIBUTION. — This species is known only from the vicinity of Danger Point in Walker Bay. It may be more widely distributed but has not been collected elsewhere, probably owing to the fact that it is found in deep water, near the margins of scuba diving depths.

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1A) are 26–55 mm in length. The body is translucent white to pale yellow with a series of reddish purple spots scattered over the surface of the notum and sides of body and foot. The rhinophores are the same color as the body. The gills are translucent white with opaque white glands at the base of each gill.

The body is high with a distinct, continuous notal ridge along the entire notal margin. Defensive glands are found along the entire notal margin (Fig. 2A), as well. The rhinophores are perfoliate with 15–19 lamellae. The branchial plume is composed of 15–18 unipinnate and bipinnate lamellae (Fig. 2B). The reproductive opening is located on the right side of the body, about one-third of the total body length posteriorly from the anterior margin of the head.

BUCCAL ARMATURE. — The jaws consist of numerous undivided rodlets (Fig. 3A). The radula of one specimen had a formula of 66 × 180–193.1.180–193. The rachidian tooth (Fig. 3B) is vestigial, narrow and linear. The inner lateral teeth lack a distinct cusp in all teeth examined. The second to eighth lateral have a well-developed cusp with a single small denticle on the outer side of the cusp. The remaining teeth all have a well-developed cusp, but lack any denticles. The teeth from the middle portion of the half-row (Fig. 3C) are more elongate that those closer to the medial portion of the radula. The outermost teeth (Fig. 3D) are shorter and also lack denticles.

REPRODUCTIVE SYSTEM. — The reproductive organs are arranged in a triaulic arrangement (Fig. 3C) typical of doridacean nudibranchs. The ampulla is thin and elongate. It branches into a short oviduct and an elongate vas deferens. The oviduct enters the female gland mass. The distal portion of the vas deferens is prostatic, elongate and convoluted. It narrows somewhat and expands again into the muscular portion, consisting of a single fold. The proximal portion of the vas deferens opens into a short penial sac which opens adjacent to the vagina. The vagina is elongate and undulate. Near its distal end it is joined by the uterine duct, which is short and enters the female gland mass. The distal end of the vagina joins the junction of the spherical bursa copulatrix and the elongate, pyriform receptaculum seminis. The female gland mass consists of three major portions: the albumen, membrane and mucous glands. The mucous gland is the largest portion. A massive vestibular gland containing many tubules is located next to the surface of the female gland mass. It exits adjacent to the vagina and the opening of the female gland mass.

DISCUSSION. — *Ceratosoma ingozi* is most similar to *C. amoena*. Both species lack a distinct posterior glandular protuberance and lack lateral extensions or undulations of the notal margin. Although both species have purple spots, they differ markedly in other aspects of their coloration. *Ceratosoma amoena* has orange spots in addition to the purple ones and purple pigment is also present on the gills and rhinophores. Internally, there are also major differences in the buccal armature. The jaw rodlets of *C. amoena* are bifid as in *Chromodoris* while those of *C. ingozi* are undivided as in the remaining species of *Ceratosoma*. The radular morphology of *C. amoena* is more similar to that of *Chromodoris*, with well-developed rachidian and cuspidate teeth with numerous denticles. In *C. ingozi*, the rachidian teeth are reduced. The innermost lateral tooth lacks a distinct cusp and only the first several inner teeth have any trace of denticulation.

Ceratosoma alleni sp. nov.
(Figs. 1B, 4, 5)

TYPE MATERIAL. — Holotype: CASIZ 085888, 2 km E. of Lighthouse, near Dakak Resort, Dapitan, northern Mindanao, Philippines, 10 m depth, 29 March 1993, Jerry Allen. Paratype, CASIZ 104200, Kirby's Rock, Maricaban Island, Batangas Province, Luzon, Philippines, 8 m depth, 19 February 1995, Michael Miller.

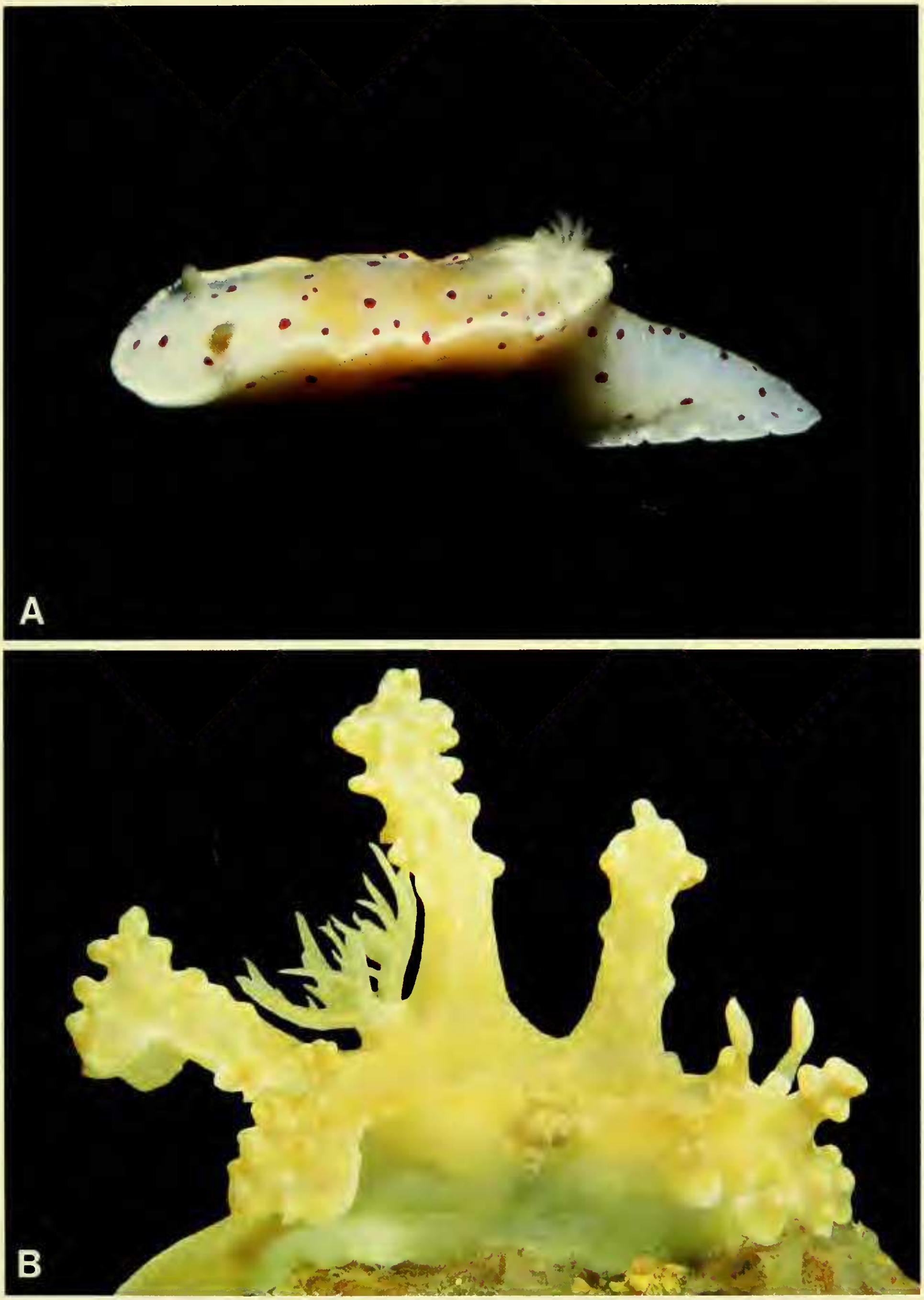

FIGURE 1. Living animals. A. *Ceratosoma ingozi* sp. nov, specimen from off Danger Point, South Africa, photo by W. R. Liltved. B. *Ceratosoma alleni*, specimen from Dakak, Mindanao, Philippines, photo by Michael Miller.

ETYMOLOGY. — *Ceratosoma alleni* is named for Jerry Allen of Tucson, Arizona, who first discovered this species on one of our joint trips to the Philippines.

DISTRIBUTION. — Thus far, this species is known only from the Mindanao and Luzon Islands in the Philippines.

EXTERNAL MORPHOLOGY. — The preserved animals are 47 and 61 mm in length. The living animals (Fig. 1B) are light brownish gray with lighter pustules over the body surface. The rhinophores are the same color as the body, but have a white apex. The gills are also brownish. The body has a rigid texture when the animal is alive.

The body shape is striking and distinctive. The head contains six pustulose, dorsoventrally flattened lobes along its anterior and lateral margins (Fig. 4A). Each of these lobes has a complex array of mantle glands on the ventral surface. Extending laterally from either side of the notum are two or three elongate, pustulose lobes with defensive glands on the ventral surface of the apical portion of the lobe (Fig. 4B). Along the median line are a series of pustulose appendages. A lobe of moderate length is present anterior to the rhinophores followed by a short lobe immediately posterior to the rhinophores. More posteriorly an elongate lobe is present followed by an even longer appendage just anterior to the gills. None of these lobes appear to contain defensive glands. Immediately posterior to the gills is an elongate, dorsoventrally flattened appendage with defensive glands. This appears to be homologous to the posterior glandular protuberance of other species of *Ceratosoma*. The rhinophores are thin and elongate with well-elevated sheaths. The rhinophores are perfoliate with 31 lamellae. The branchial plume is composed of 6–10 bipinnate lamellae. The reproductive opening is located on the right side of the body, about one-third of the total body length posteriorly from the anterior margin of the head.

BUCCAL MASS AND ARMATURE. — The buccal mass (Fig. 4C) consists of a largely muscular posterior portion and a glandular anterior one. At the junction of these two portions are three large lateral muscles on either side of the mass. A large, strap-like salivary gland is present on each side of the posterior end of the buccal mass, adjacent to the junction of the esophagus with the buccal mass.

The jaws consist of numerous elongate, undivided rodlets (Fig 5A). The radula of the paratype had a formula of $77 \times 93–108.0.93–108$. No trace of a rachidian tooth was observed. The inner lateral teeth (Fig. 5B) lack denticles on the inner side of the cusp, but have 1–3 rounded denticles on the outer side of the cusp. The second to seventh laterals have traces of denticular tubercles on the outer edges. The remaining teeth all have a well-developed cusp, but lack any denticles. The teeth from the middle portion of the half-row (Fig. 5C) are more elongate and curved than those closer to the medial portion of the radula. The outermost teeth (Fig. 5D) are shorter and also lack denticles.

REPRODUCTIVE SYSTEM. — The reproductive organs are arranged in a triaulic arrangement (Fig. 4D). The ampulla consists of several convolutions. It branches into a moderately short oviduct and an elongate vas deferens. The oviduct enters the female gland mass. The distal portion of the vas deferens is prostatic, elongate and convoluted. It narrows somewhat and expands again into the muscular portion, consisting of a single fold. At the point where the muscular portion loops back upon itself, the vas deferens penetrates the muscular portion of the dorsal body wall and re-emerges back into the body cavity. The proximal portion of the vas deferens opens into a moderately elongate penial sac which opens adjacent to the vagina. The vagina is elongate and convoluted. Near its distal end it is joined by the uterine duct, which is short and enters the female gland mass. The distal end of the vagina joins the junction of the spherical bursa copulatrix and the elongate, pyriform receptaculum seminis. The female gland mass consists of three major portions: the albumen, membrane and mucous glands. The mucous gland is the largest portion. A vestibular gland appears to be entirely absent.

DISCUSSION. — The external morphology of *Ceratosoma alleni* is unique among described species of *Ceratosoma*. It is the only species with prolonged lateral extensions of the notum which contain glandular arrays on the ventral surface. It is also the only species with elongate medial appendages in addition to the posterior glandular protuberance. The only other species with tuberculate pustules is *C. moloch* Rudman, 1988. This species is red in color and has de-

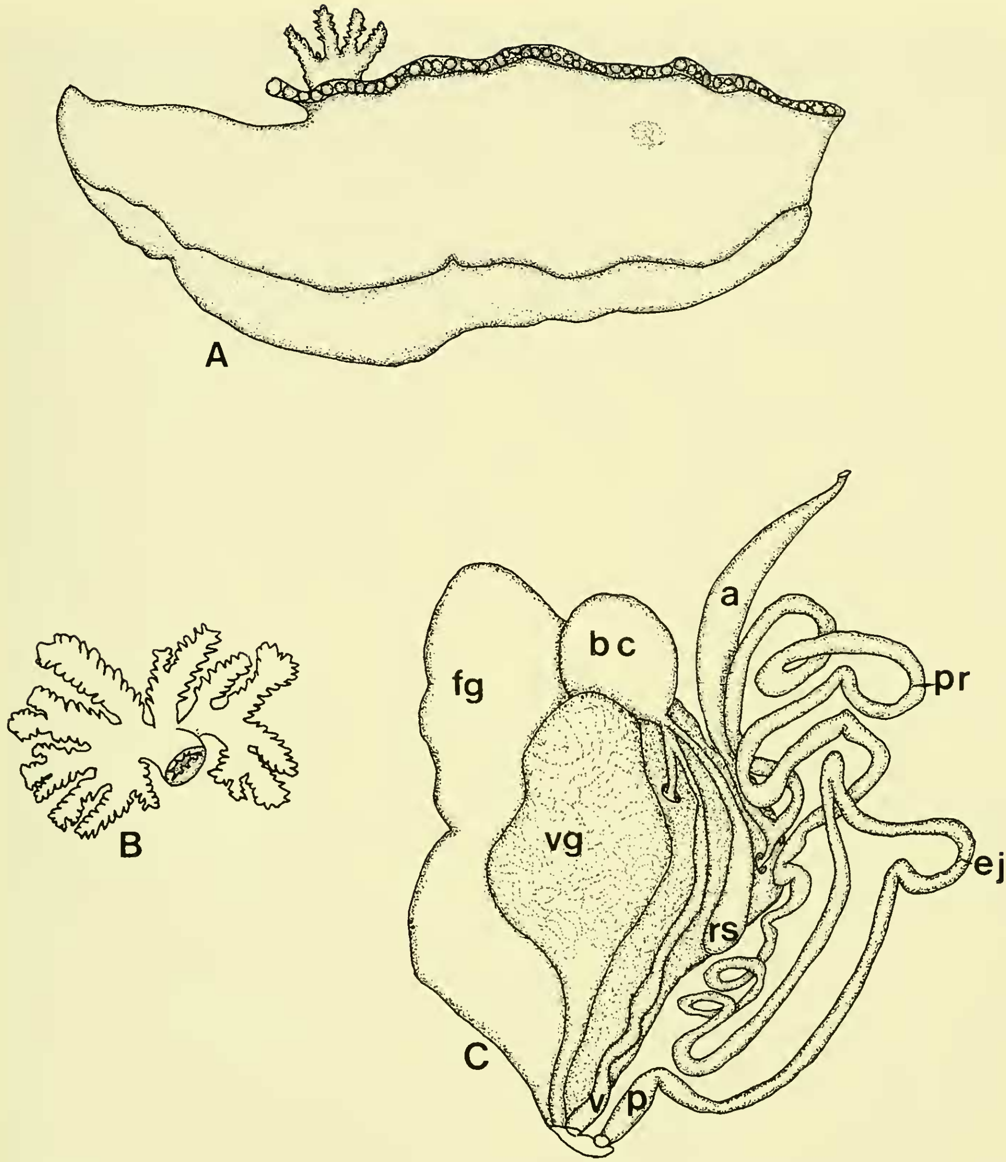

FIGURE 2. *Ceratosoma ingozi* sp. nov. A. General body shape showing distribution of mantle glands. B. Branching of gills. C. Arrangement of reproductive organs, a = ampulla; bc = bursa copulatrix; ej = ejaculatory portion of vas deferens; fg = female gland mass; p = penis; pr = prostatic portion of vas deferens; rs = receptaculum seminis; v = vagina, vg = vestibular gland.

fensive glands all over the surface of the pustules. *Ceratosoma alleni* has several denticles on the outside of the innermost teeth while a single denticle is present on the inner lateral tooth of *C. moloch*. The teeth from the middle of the half-row of *C. alleni* lack denticles while those of *C. moloch* bear 3–5 denticles. The reproductive system of *C. alleni* appears to lack a vestibular gland, while that of *C. moloch* is typical of *Ceratosoma* species with a large saccate gland.

Ceratosoma alleni closely resembles an unidentified xeniid soft coral which has been found in the same habitat. This species may

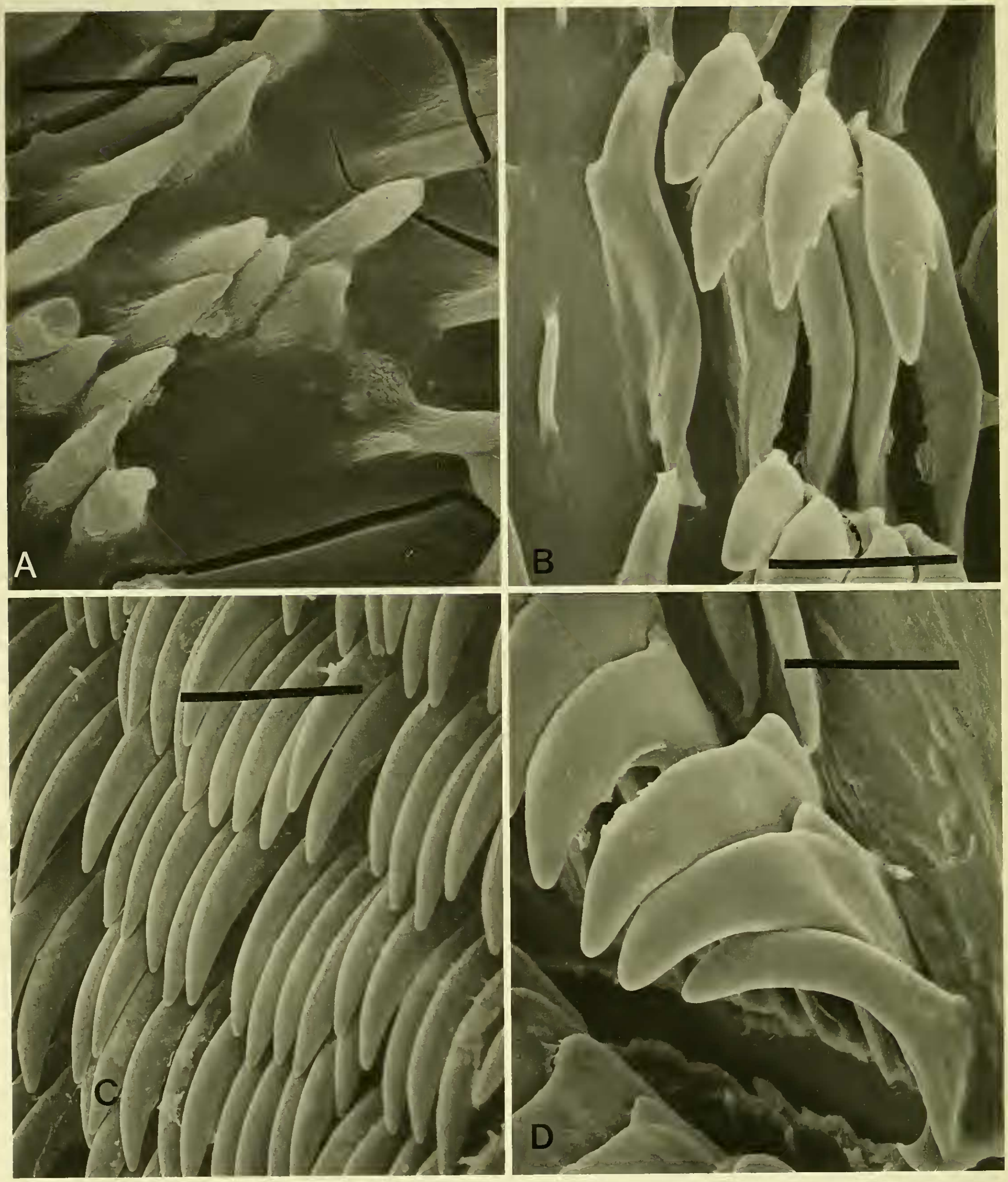

FIGURE 3. *Ceratosoma ingozi* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 10 µm. B. Rachidian and inner lateral teeth, scale = 43 µm. C. Teeth from central portion of half-row, scale = 100 µm. D. Outer lateral teeth, scale = 43 µm.

closely resemble the soft coral to elude visual predators. Although *C. alleni* has not been observed feeding, it is probable that it feeds upon sponges, like other chromodorids, rather than feeding upon soft corals.

PHYLOGENETIC RELATIONSHIPS

Rudman's (1988) review provides a wealth of characters for the study of phylogenetic relationships of the species of *Ceratosoma*. He

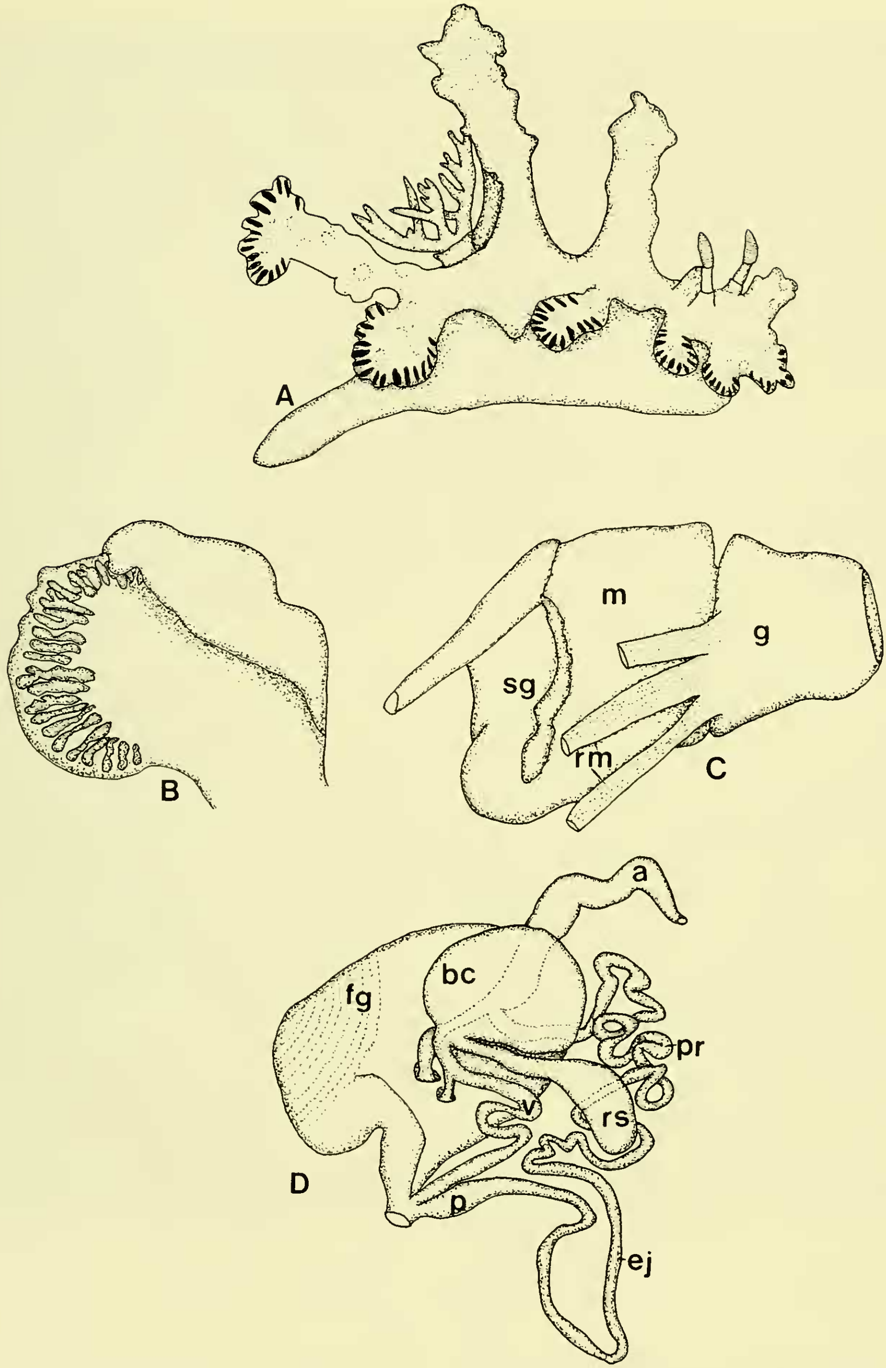

FIGURE 4. *Ceratosoma alleni* sp. nov. A. Distribution of mantle glands over body surface. B. Distribution of mantle glands on left posterior appendage. C. Buccal mass, g = glandular portion; m = muscular portion; rm = retractor muscles; sg = salivary gland. D. Reproductive system, a = ampulla; bc = bursa copulatrix; ej = ejaculatory portion of vas deferens; fg = female gland mass; p = penis; pr = prostatic portion of vas deferens; rs = receptaculum seminis; v = vagina.

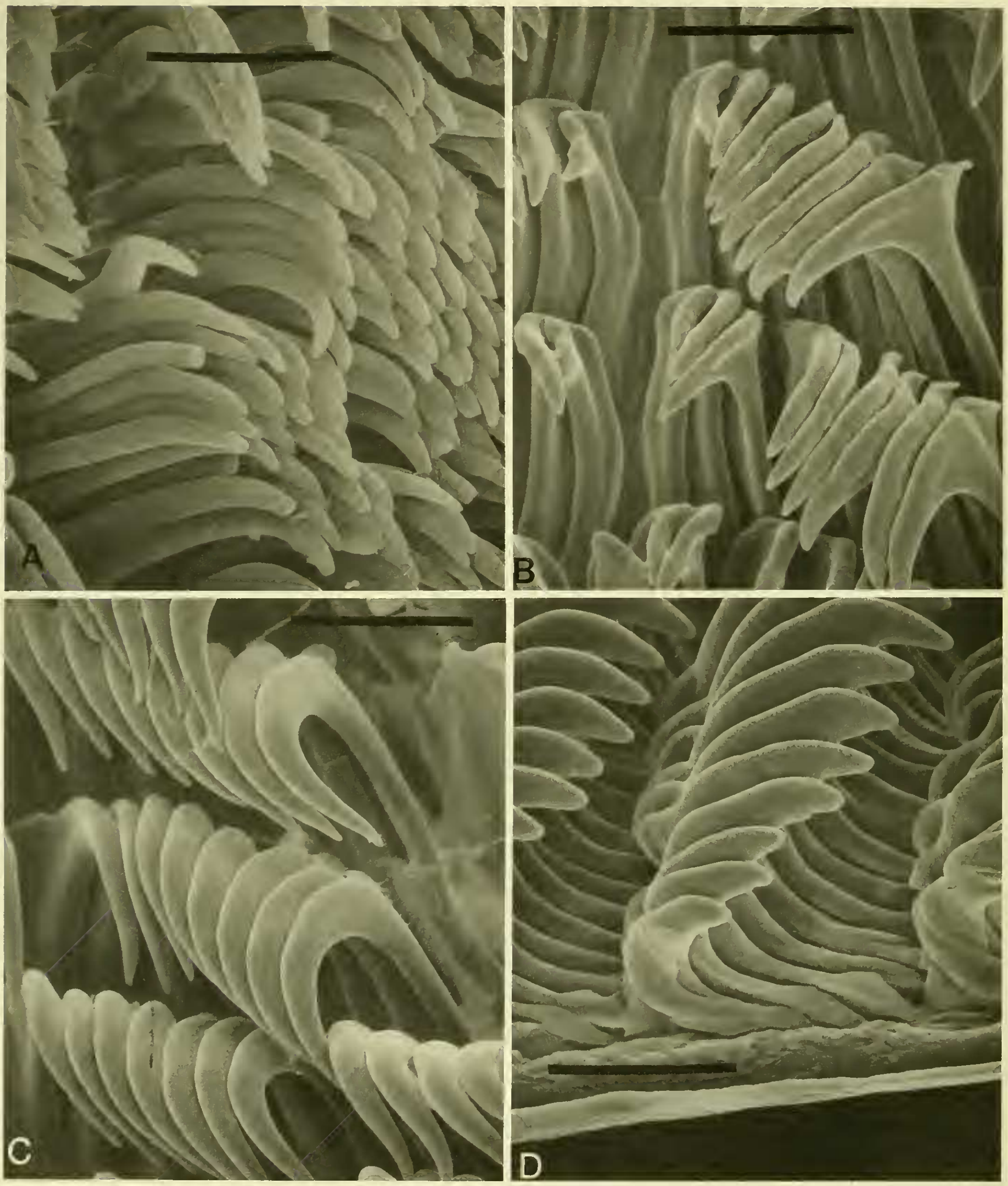

FIGURE 5. *Ceratosoma alleni* sp. nov. Scanning electron micrographs. A. Jaw rodlets, scale = 20 μm. B. Rachidian and inner lateral teeth, scale = 60 μm. C. Teeth from central portion of half-row, scale = 60 μm. D. Outer lateral teeth, scale = 43 μm.

noted that radular characters of some species of *Ceratosoma* demonstrate a more plesiomorphic condition earlier in their ontogeny while adults exhibit only the derived condition. He also discussed evolutionary trends of radular, mantle and defensive gland morphology, but did not present an explicit phylogeny of species relationships within the genus.

In order to polarize the morphological variability of species of *Ceratosoma* it is necessary to select outgroups. For this purpose, species of *Chromodoris* and *Hypselodoris* were selected, as they contain taxa with more plesiomorphic morphology and are sufficiently diverse to represent the morphological variation contained within *Ceratosoma*. Rudman (1984) has hypothesized that relationships of *Ceratosoma* to *Hypselodoris*, and considers *Hypselodoris* to be derived from a *Chromodoris* relative. The following characters (Table 1) were considered in undertaking a phylogenetic analysis:

1. Body profile. — Species of *Chromodoris* have a low body profile while all *Hypselodoris* and *Ceratosoma* have a high body profile. The condition present in *Chromodoris* is like that found in other cryptobranch dorids and is considered plesiomorphic.

2. Body firmness. — All species of *Chromodoris* and *Hypselodoris* have a soft, fleshy body; species of *Ceratosoma* have a firm and rubbery body. A more rigid body appears to be apomorphic.

3. Body texture. — Virtually all species of *Chromodoris*, *Hypselodoris* and *Ceratosoma* have a smooth body texture. *Ceratosoma moloch* and *C. alleni* have pustules over the body surface. Presence of pustules is considered the apomorphic state.

4. Notal margin. — In species of *Chromodoris*, *Hypselodoris* and most *Ceratosoma* the edge of the notum forms a continuous rim around the entire margin of the animal. In *Ceratosoma gracillimum* and *C. tenue* the mantle margin contains areas of discontinuity. A discontinuous mantle is considered apomorphic.

5. Mantle lobes. — The mantle margin of *Chromodoris*, *Hypselodoris* and some species of *Ceratosoma* is straight, without any undulations. In all species of *Ceratosoma*, except *C. amoena* and *C. ingozi*, the mantle margin contains permanent undulations or lobe-like extensions. An undulating mantle margin is considered apomorphic.

6. Posterior protuberance. — The posterior end of the mantle of *Chromodoris*, *Hypselodoris*, *Ceratosoma amoena*, *C. ingozi* and *C. palliolatum* is undifferentiated from the rest of the notal margin. In the remaining species of *Ceratosoma*, an extended lobe, containing concentrated defensive glands, is present and is considered apomorphic.

7. Mantle glands. — Mantle glands in *Chromodoris*, *Hypselodoris* and several species of *Ceratosoma* are distributed around the entire margin of the notum. In *Ceratosoma gracillimum*, *C. trilobatum* and *C. tenue*, mantle glands are present only along the margin of the head and at the apex of the posterior protuberance. In *Ceratosoma alleni*, mantle glands are present along the margin of the head, at the apex of the posterior protuberance and at the apices of the lateral mantle lobes. Both of the later arrangements are considered apomorphic. This character is treated as unordered in the analysis.

8. Gills. — The gills in species of *Chromodoris*, *Hypselodoris* and *Ceratosoma amoena* are unipinnate while those of the remaining species of *Ceratosoma* contain at least some bipinnate gills. Presence of bipinnate gills is considered apomorphic.

9. Jaw elements. — In *Chromodoris* and *Ceratosoma amoena*, the jaw rodlets are bifid. In *Hypselodoris* and adult specimens of the remaining species of *Ceratosoma*, the jaw rodlets are largely undivided. In juvenile specimens of *C. brevicaudatum*, there are more bifid rodlets that in adults. A few of the rodlets in adult specimens of *C. palliolatum* and *C. brevicaudatum* are occasionally bifid. Having mostly undivided rodlets is considered apomorphic.

10. Rachidian teeth. — In most species of *Chromodoris*, some *Hypselodoris* and some *Ceratosoma*, a distinct row of rachidian teeth is present. In some instances the rachidian teeth are prominent while in other cases they are reduced in size and are considered vestigial. In *Ceratosoma tenue* and *C. alleni* no vestige of a rachidian is apparent. The absence of rachidian teeth is considered apomorphic.

11. Outer lateral teeth. — The outer lateral teeth of *Chromodoris*, most species of *Hyp-*

TABLE 1. Character states in *Chromodoris*, *Hypselodoris* and *Ceratosoma*.

	Character															
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chromordoris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypselodoris	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0
amoena	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1
brevicaudatum	1	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1
gracillimum	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	1
moloch	1	1	1	0	1	1	0	1	1	0	1	0	1	0	1	1
palliolatum	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1
trilobatum	1	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1
tenue	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1
ingozi	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1
alleni	1	1	1	0	1	1	2	1	1	1	1	0	2	0	1	1

0 = plesiomorphic condition
1, 2 = apomorphic condition

selodoris and most species of *Ceratosoma* bear small denticles. In *Ceratosoma gracillimum*, *C. moloch*, *C. trilobatum*, *C. ingozi* and *C. alleni*, all of the outer lateral teeth are smooth, without denticles. This morphology is considered apomorphic.

12. Tooth denticulation. — In species of *Chromodoris* and *Ceratosoma* the radular teeth have a single primary cusp, while in *Hypselodoris* all the teeth have a bifid cusp. The arrangement found in *Hypselodoris* is considered apomorphic.

13. Vestibular gland size. — In *Chromodoris* the vestibular gland is small and simple. In *Hypselodoris* and most species of *Ceratosoma*, the vestibular gland is greatly enlarged. In *C. alleni*, a vestibular gland appears to be entirely absent. An enlarged vestibular gland and a lack of a vestibular gland are both considered to represent apomorphic conditions. The character is treated as unordered in the analysis.

14. Vestibular gland shape. — In *Chromodoris* and *Ceratosoma*, the vestibular gland is saccate. In species of *Hypselodoris* the vestibular gland is highly ramified. The latter form is considered apomorphic.

15. Vagina. — The vaginal duct of species of *Chromodoris* and *Hypselodoris* is relatively short and thick while in *Ceratosoma* it is far more thin and elongate. A more elongate vagina is considered apomorphic.

16. Prostate. — In *Chromodoris* and *Hypselodoris*, the prostatic portion of the vas deferens is relatively short. In *Ceratosoma*, the prostatic portion consists of far more folds and convolutions and is considered apomorphic.

In order to develop phylogenetic hypotheses regarding these taxa, the above described characters were placed in a data matrix (Table 1) and analyzed by means of Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1, by David Swofford. A single most parsimonious tree was produced (Fig. 6). This tree requires 22 steps and has a consistency index of 0.818.

In the above scenario, only two characters exhibit homoplasy. The loss of denticulation of the outer lateral teeth has occurred independently in *Ceratosoma ingozi* and again in the clade containing *C. gracillimum*, *C. trilobatum*, *C. tenue*, *C. moloch* and *C. alleni*. Within that clade, a reversal to plesiomorphically denticulate outer teeth has occurred in *C. tenue*. Also, undivided jaw rodlets have originated in

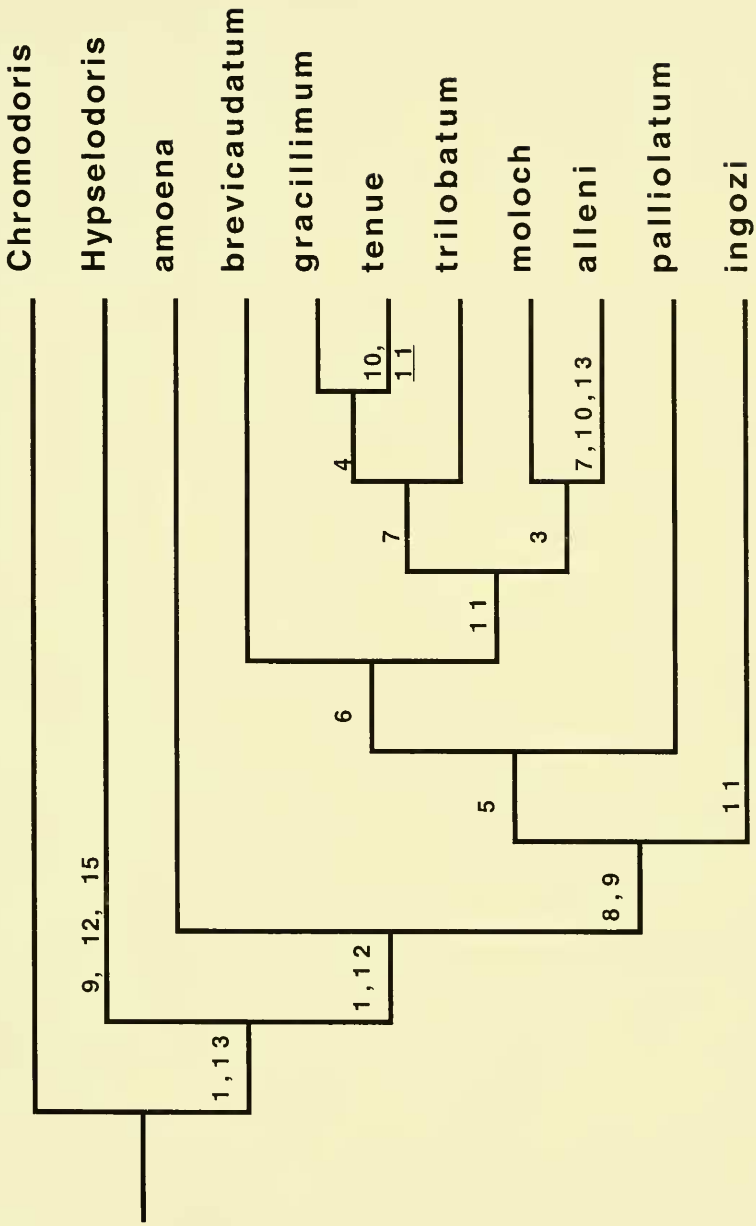

FIGURE 6. Hypothesis of phylogeny of species of *Ceratosoma*. Numbers refer to characters listed within text.

Hypselodoris and again in most species of *Ceratosoma*.

ACKNOWLEDGMENTS

I thank Jerry Allen and Mike Miller for finding the specimens of *Ceratosoma alleni* and for making their photographs of this species available for publication. Bill Liltved endured rigorous diving conditions to collect specimens of *Ceratosoma ingozi*. His continued support of research efforts on the South African molluscan fauna is greatly appreciated. Travel support for field studies in the Philippines was kindly provided through the generous support of Katharine Stewart and the Lindsay Field Research Fund of the California Academy of Sciences and United Airlines. The Photography Department of the California Academy of Sciences kindly printed the black and white photographs used in this paper.

LITERATURE CITED

BABA, K. 1989. Review of the genus *Ceratosoma* from Japan (Nudibranchia: Chromodorididae). Venus 48(3):141–149.

GOSLINER, T. 1987. Nudibranchs of Southern Africa. A guide to the opisthobranch molluscs of southern Africa. Sea Challengers, Monterey, 136 pp.

RUDMAN, W. B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zoological of the Linnean Society 81:115–273.

———. 1988. The Chromodorididae (Opisthobranchia: Mollusca) from the Indo-West Pacific: the genus *Ceratosoma* J. E. Gray. Zoological Journal of the Linnean Society 93:133–185.